Effect of Rearing Strategy and Gamma Radiation on Field Competitiveness of Mass-Reared Codling Moths (Lepidoptera: Tortricidae)

STEPHANIE BLOEM,[1] JAMES E. CARPENTER,[2] KENNETH A. BLOEM,[3] LORNE TOMLIN,[4] and SHANNON TAGGART[4]

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ABSTRACT We compared the field competitiveness of sterile codling moth, *Cydia pomonella* (L.), males mass-reared through diapause or standard production protocols and treated with either 150 or 250 Gy of gamma radiation. Evaluations were performed during spring and summer 2003 by using field release–recapture tests. Released males were recaptured using traps baited with synthetic pheromone or with virgin females. In addition, mating tables baited with virgin females were used in the summer to assess the mating competitiveness of the released moths. Field performance of released males was significantly improved by rearing through diapause and by lowering the dose of radiation used to treat the insects. These effects were observed during spring when evening temperatures were relatively cool and in summer when evening temperatures were high. These effects were observed regardless of the sampling method (i.e., capture in pheromone-baited traps, virgin female-baited traps, or in mating tables). There were significant interactions between larval rearing strategy and radiation dose with respect to day of recapture. The effect of rearing strategy on male performance was observed immediately after release, whereas the effect of dose of radiation was usually delayed by 2–3 d. In general, the best treatment for improving codling moth male field performance was a combination of rearing through diapause and using a low dose of radiation (150 Gy). The difference in performance when insects were treated with 150 or 250 Gy was greater when males had been reared using standard (nondiapause) rearing protocols, suggesting that diapause rearing may attenuate some of the negative effects of the higher doses of radiation.

KEY WORDS codling moth, sterile insect technique, competitiveness, trapping, diapause

The current objective of the Sterile Insect Release (SIR) Program in British Columbia, Canada, is areawide suppression of the codling moth, *Cydia pomonella* (L.), the key pest of apples (*Malus* spp.) and pears (*Pyrus* spp.), in the fruit-growing valleys of the interior of British Columbia (Bloem and Bloem 2000). The program was launched in 1992 after rising chemical costs, threat of pesticide resistance, and increasing concern about environmental and worker-safety issues brought the costs versus benefits of sterile insect release more into line with those of traditional control programs (Dyck et al. 1993). Since its inception, the SIR Program has significantly reduced both the use of organophosphate cover sprays (by 82% of preprogram levels) and the feral codling moth population (by 95%) in the initial 3,200-ha treatment area. Nevertheless, the long-term sustainability of the program continues to be debated (Dendy et al. 2001).

Maintaining or improving the quality of mass-reared laboratory-adapted insects is essential if programs using the sterile insect technique are to be successful (Calkins and Ashley 1989). According to Huettel (1976), the quality of a laboratory population is measured by how well it functions in its intended role (i.e., how effectively in interacts with and impacts upon the target population). For codling moth, Proverbs (1971) documented that laboratory insects reared at constant high temperature were less active in the spring compared with feral moths that overwintered in the orchard. Bloem et al. (1997) investigated the possibility of incorporating diapause into codling moth mass rearing as a way of improving codling moth quality, particularly during releases of sterile moths at the beginning of the growing season when field temperatures are cool. Bloem et al. (1997) showed that adult codling moths reared through diapause were of comparable quality to standard-reared (nondiapaused) colony in-

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[1] Center for Biological Control, Florida A&M University, Tallahassee, FL 32308.

[2] USDA–ARS, Crop Protection & Management Research Unit, Tifton, GA 31793.

[3] USDA–APHIS–PPQ–CPHST–Center for Biological Control, Florida A&M University, Tallahassee, FL 32307.

[4] Okanagan-Kootenay Sterile Insect Release Program, Osoyoos, British Columbia, V0H1V0, Canada.

sects when longevity, size, and mating ability were measured in the laboratory. Subsequently, Bloem et al. (1998) reported that field performance of codling moths reared through diapause was significantly higher than that of moths reared under standard (nondiapaused) protocols and treated with the same high dose of gamma radiation (330 Gy). More recently, Bloem et al. (1999a, b, 2001) have demonstrated that mass-reared codling moths treated with lower doses of radiation are significantly more competitive than those treated with higher doses. Bloem et al. (1999a) reported that female codling moths are completely sterilized at a dose of 100 Gy, whereas males are partially sterile at this dose. An areawide program that releases fully sterile females and partially sterile male moths can take advantage of the phenomenon of inherited sterility (North 1975, LaChance 1985) to bring about population control more quickly than releasing fully sterile males and females (Bloem and Carpenter 2001).

In an effort to continue to find ways of improving the quality of laboratory-adapted mass-reared codling moths, we compared the quality of standard (nondiapaused) and diapaused reared codling moths treated with two substerilizing doses of gamma radiation (150 and 250 Gy) in large-scale release-recapture tests in the spring and summer 2003 in apple orchards in British Columbia. Released males were recaptured using traps baited with synthetic pheromone or with virgin females. Furthermore, mating tables (Bloem et al. 1999b) were used in the summer to assess the mating competitiveness of the released male moths. Differences in the hourly capture of male codling moths in pheromone-baited and virgin female-baited Delta traps also were examined in the summer. Results of these experiments are presented herein, and the importance of the data to the implementation of a successful areawide sterile insect release program for codling moth is discussed.

Materials and Methods

Test Insects. The codling moth colony used in these experiments has been in continuous culture since 1993 (≈10 generations per year), although routine introduction of 50–100% feral males is made into the colony in the winter of most years. Colony insects are mass reared on a modified sawdust-based artificial diet originally developed by Brinton et al. (1969). The rearing facility located in Osoyoos, British Columbia, routinely produces 14–15 million codling moths per week.

Two mass-rearing strategies (standard and diapause) and two different doses of radiation (150 and 250 Gy) were used to prepare the insects used in these experiments. For standard rearing, codling moth eggs were placed on trays of artificial diet and reared in walk-in rooms at constant temperature (27°C), a photoperiod of 16:8 (L:D) h, and 55% RH for 21 d. At day 22, trays with mature larvae and early pupae were moved into adult emergence rooms (27°C, 30% RH, and a photoperiod of 16:8 [L:D] h). At day 30, the start of adult eclosion, the photoperiod was shifted to 0:24 (L:D) h. UV lights attached to wind traps in the ceiling of emergence rooms were turned on for 50 min every hour, and moths attracted to the light were transported through ducts to a cold room (0–2°C). Only adult moths that were <24 h old were used for field release.

Diapause was induced in neonate larvae in fall 2002 by shortening the photoperiod and lowering the temperature (12L-25°C:12D-21°C) during larval rearing; relative humidity remained at 55%. Larvae reared under the diapause conditions were collected into corrugated cardboard pallets, conditioned (at 15°C and 0L:24D for a minimum of 100 d), and stored (at 0–2°C and 0L:24D for a minimum of 30 d) as outlined in Bloem et al. (2000). After several months in cold storage, diapause was broken by placing the larvae in cardboard emergence boxes (100 by 55 by 80 cm) at 27°C and a photoperiod of 16:8 (L:D) h. Emerging adults were collected once every 2 h and stored in a cold room (0–2°C). As stated above, only adult moths that were <24 h old were used for field release.

Adult moths produced through standard and diapause rearing were each divided into two groups and marked with distinguishing fluorescent dusts (Day-Glo Color, Cleveland, OH) at the rate of 5 mg per 23 g of adults. Adults were packaged into plastic petri dishes as follows. For standard rearing, 23 g of adults per dish (≈820 adults, mean weight 28 mg, and sex ratio 1:1) and for diapaused moths 20 g of adults per dish (≈808 adults, mean weight 24.75 mg, and sex ratio 1:1). One group from each rearing strategy (standard and diapaused) was treated with 150 Gy, and the other group was treated with 250 Gy of gamma radiation from a Cobalt^{60} source (Gammacell 220, Nordion, Canada; dose rate of 0.749448 Mrad/h in May 2003 and 0.7331184 Mrad/h in July 2003). After irradiation, all moths were maintained in the cold room (0–2°C) until released in the field.

Traps and Sites. The studies were conducted in spring (May) and summer (July) 2003 in a 20-ha mixed high-density (Gala and Fuji) and traditional planting (Granny Smith and Red Delicious) apple orchard on the southwestern side of Lake Osoyoos in British Columbia, Canada. Tree spacing was 2.00 by 4.25 m (≈1,175 trees per hectare) in the high-density plots and 4.40 by 6.00 m (≈400 trees per hectare) in the traditional plantings. Mean tree height throughout the orchard was 2.75–3.60 m. Captures of standard and diapaused codling moths were assessed using two different trap types: 1) pheromone-baited (1 mg of codlemone) wing traps (Tecpak Packaging Ltd., Oliver, British Columbia, Canada) used in spring and summer evaluations and 2) virgin female-baited wing traps used only in the summer experiments. In the female-baited traps, the pheromone lures were replaced with modified plastic film canisters that held individual 2-d-old virgin females. Water-soaked cotton wicks affixed to the bottoms of the canisters provided moisture to the caged females. Five pheromone-baited traps and 16 virgin female-baited traps were used per hectare. All traps were evenly spaced throughout the plots and hung in the upper one-third of the tree canopy (mean trap height 2 m) on the day of release. Field temperatures were recorded every hour for the duration of the study by using electronic data pods (HOBO, Onset, Bourne, MA).

Releases and Trap Servicing. Releases occurred along three marked lanes ≈30 m apart in four 1-ha high-density plots, each separated by at least 100 m from other release plots. A single release was made in spring (2 May) and in summer (10 July) 2003. Standard and diapaused codling moths were transported to the field in a small cooler, and the treatment groups were released in the morning (≈1130 hours [PST]) by using an all-terrain vehicle fitted with a moth-dispensing unit, which gently blew the moths into the vegetation underneath the tree canopy as the driver drove through the plots. To avoid fluorescent color contamination, the moth-dispensing unit was wiped clean between releases. Release order for the different treatments was chosen at random. For standard moths (treated with 150 and 250 Gy), 46 g (≈1,640 adults, mean weight 28 mg, and sex ratio 1:1) of each treatment were liberated per hectare and for diapaused moths (treated with 150 and 250 Gy) 40 g (≈1,616 adults, mean weight 24.75 mg, and sex ratio 1:1) of each treatment were released per hectare along the three release lanes.

Traps were checked daily for 8–11d after moth releases. New sticky trap bottoms were placed in traps that had captured at least one moth. At day 5 after release, females in virgin female-baited traps were replaced with fresh, 2-d-old females. A UV light was used to identify the color and thus the treatment of trapped codling moths. Higher trap captures were interpreted as indicative of higher moth quality.

Capture of Males in Copula. Mating tables, similar to those described in Bloem et al. (1999b) were used to assess the mating competitiveness of released males during the summer. Two replicates were conducted using two traditional planted 1-ha (Granny Smith and Red Delicious) plots. Insects were released as described above. Thirty-two mating tables were hung evenly throughout each plot (total of 64 tables) in the middle one-third of the tree canopy (mean trap height 1.5m) on the day of release. Two-day-old virgin female moths were chilled in the laboratory (0–2°C), and two-thirds of the anterior right wing was carefully removed with small scissors to prevent flight. Clipped-wing females were stored in small plastic cups (29.5 ml), transported to the field in a cooler, and an individual female was placed inside the mating arena of each table at ≈1600 hours (PST) on a given observation day.

Mating tables were visited once per hour, from 1700 to 0200 hours (PST), and pairs found in copula were collected into small cups (29.5 ml). The hour during which each mating pair was collected was noted. The color and thus the treatment of the male captured in copula with the female was identified under UV light. The experiment was conducted nightly for five nights, 10–14 July 2003.

Hourly Trap Captures. As stated above, 46 g of standard and 40 g of diapaused moths were released into an additional 1-ha traditional planted plot in the summer (10 July). Five pair of pheromone-baited and virgin female-baited Delta traps (Pherocon VI, Trécé, Adair, OK) were hung throughout the plot at evenly spaced locations. The position of each trap type at each location was chosen at random, and the traps were placed in the upper one-third of the canopy (mean trap height 1.75 m) and separated from one another by 10 m. Traps were visited once per hour between 1700 and 0100 hours (PST) for 3 d (10–12 July 2003), and the number of moths caught in each trap type was recorded.

Data Analysis. The number (and $\log_{10}$-transformed number) of codling moth males captured in pheromone-baited traps during the spring (May) and summer (July) experiments was analyzed using a three-factor analysis of variance (ANOVA) with day of capture, insect rearing strategy, and dose of radiation as sources of variation. A nested blocking effect of plot and trap position within each plot was used in the analysis (PROC ANOVA) (SAS Institute 1989). Because a significant three-way interaction between day of recapture, insect rearing strategy, and dose of radiation for the spring and summer data were found, the number (and $\log_{10}$-transformed number) of males captured in the pheromone-baited traps was sorted by day of recapture and analyzed using a two-factor ANOVA with insect rearing strategy and dose of radiation as sources of variation. A nested blocking effect of plot and trap position within each plot (PROC ANOVA) (SAS Institute 1989) also was used here. All interactions were included in the statistical model. A similar model was used to analyze the number (and square root and $\log_{10}$-transformed number) of codling moth males recaptured in virgin female-baited traps during the summer experiment. The number of males found in copula with females placed in the mating tables was subjected to a two-factor ANOVA with rearing strategy and dose of radiation as sources of variation and blocked by day of capture and time of mating. Because no interactions were detected and no effect due to day of capture was found, treatment means were compared with a Student's t-test by using the five capture days as replicates. Finally, the number of males captured per hour in pheromone-baited and in virgin female-baited traps was subjected to ANOVA with a blocking effect of trap type and time of capture. All interactions were included in the statistical model.

Results

The daily recapture of male codling moths in pheromone-baited traps was significantly influenced by rearing strategy (standard or diapaused) and dose of radiation (150 or 250 Gy). During the spring experiment (May 2003), the number of diapaused males that were recaptured exceeded the number of standard-reared males in 7 of 10 d, with this difference being significant on day 1 ($F = 4.99$; df = 1, 48; $P < 0.0302$), day 2 ($F = 8.54$; df = 1, 48; $P < 0.0053$), day 7 ($F = 9.96$; df = 1, 48; $P < 0.0028$), day 8 ($F = 12.97$; df = 1, 48; $P < 0.0007$), and day 9 ($F = 7.07$; df = 1, 48; $P < 0.0106$)

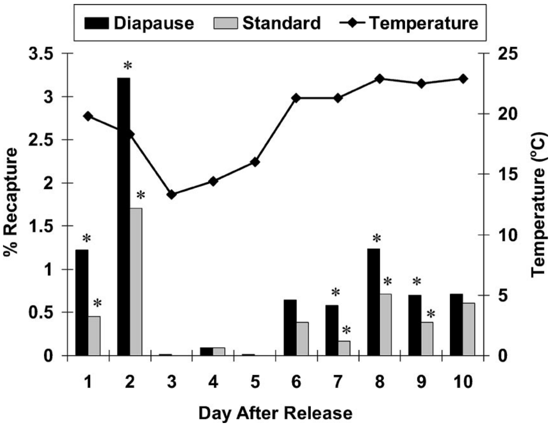

Fig. 1. Effect of mass-rearing strategy (diapause or standard) on the percentage of recapture by day of *C. pomonella* males in pheromone-baited (1 mg of codlemone) wing traps in May 2003. Approximately 3,260 males of each treatment were released per hectare on 2 May 2003 into four 1-ha plots. Trap density was five traps per hectare, which represented 20 traps total. Temperature line shows mean nightly temperature during the experiment. Means within each day denoted by asterisk are significantly different (PROC ANOVA; P = 0.05).

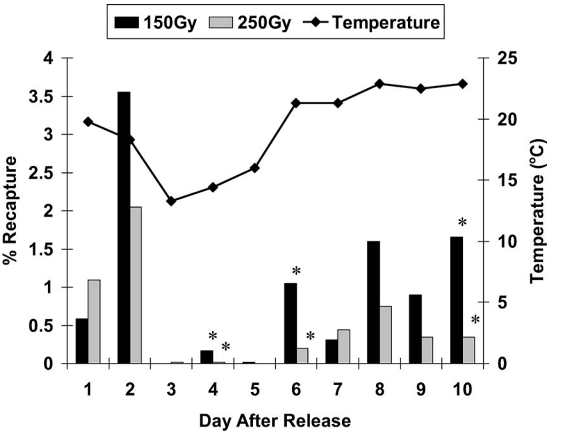

Fig. 2. Effect of dose of radiation (150 or 250 Gy) on the percentage of recapture by day of *C. pomonella* males in pheromone-baited (1 mg of codlemone) wing traps in May 2003. Approximately 3,260 males of each treatment were released per hectare on 2 May 2003 into four 1-ha plots. Trap density was five traps per hectare, which represented 20 traps total. Temperature line shows mean nightly temperature during the experiment. Means within each day denoted by asterisk are significantly different (PROC ANOVA; $P = 0.05$).

after release (Fig. 1). Similarly, the number of 150-Gy-treated males recaptured exceeded the number of 250-Gy-treated males captured in 7 of 10 days, and this difference was significant on day 4 ($F = 8.07$; df = 1, 48; $P < 0.0066$), day 6 ($F = 4.50$; df = 1, 48; $P < 0.0390$), and day 10 ($F = 9.95$; df = 1, 48; $P < 0.0028$) after release (Fig. 2). The spring data suggest that the effect on trap capture due to dose of radiation was slightly delayed with respect to the effect due to rearing strategy of the released moths (Figs. 1 and 2). In general, the ability to recapture all male treatments was reduced or limited in the spring by low evening temperatures, especially on days 3–5 when mean evening temperatures were 13.5–15.0°C. Nevertheless, significantly more 150-Gy-treated males were recaptured on day 4 than were 250-Gy-treated males (Fig. 2).

Rearing strategy and dose of radiation also significantly influenced the number of males recaptured in pheromone-baited traps in the summer trial (July 2003). Similar to the results obtained in the spring, the number of diapaused males captured exceeded the number of standard-reared males captured on each day of the trial, with the difference being significant on day 1 ($F = 14.63$; df = 1, 48; $P < 0.0004$), day 2 ($F = 30.30$; df = 1, 48; $P < 0.0001$), day 3 ($F = 5.25$; df = 1, 48; $P < 0.0264$), and day 5 ($F = 4.43$; df = 1, 48; $P < 0.0405$) (Fig. 3). Also, the number of 150-Gy-treated males captured in the summer exceeded the number of 250-Gy-treated males in nine of 11 d, with the difference being significant on day 4 ($F = 20.05$; df = 1, 48; $P < 0.0001$) and day 5 ($F = 4.36$; df = 1, 48; $P < 0.0422$) (Fig. 4). As stated above, the effect on trap capture due to dose of radiation was slightly delayed with respect to the effect due to rearing strategy (Figs. 3 and 4). Evening temperatures were higher during the summer (mean temperature was never lower than 25°C; Figs. 3 and 4) and did not limit male moth activity.

Rearing strategy and the dose of radiation also significantly influenced the number of male codling moths recaptured in virgin female-baited traps in the summer (July 2003). The number of diapaused males exceeded the number of standard-reared males that

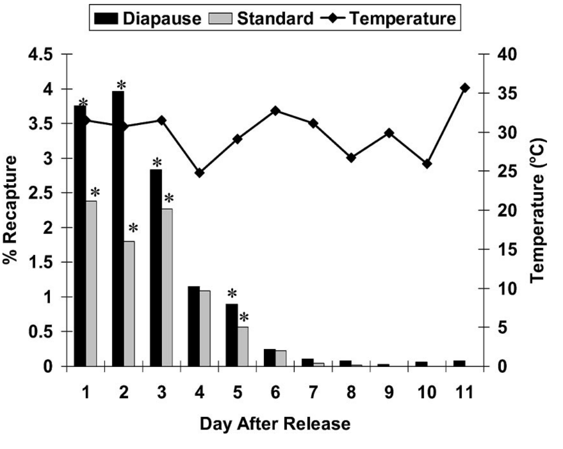

Fig. 3. Effect of mass-rearing strategy (diapause or standard) on the percentage of recapture by day of *C. pomonella* males in pheromone-baited (1 mg of codlemone) wing traps in July 2003. Approximately 3,260 males of each treatment were released per hectare on 10 July 2003 into four 1-ha plots. Trap density was five traps per hectare, which represented 20 traps total. Temperature line shows mean nightly temperature during the experiment. Means within each day denoted by asterisk are significantly different (PROC ANOVA; P = 0.05).

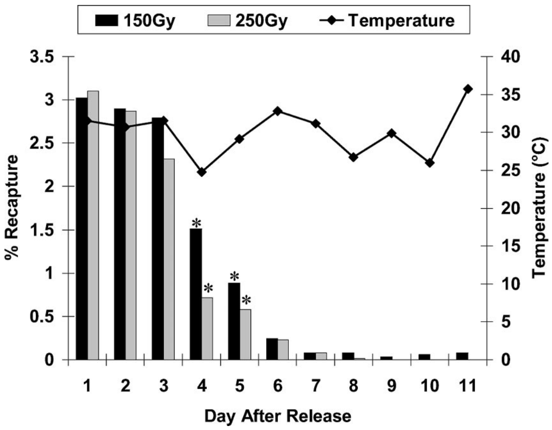

Fig. 4. Effect of dose of radiation (150 or 250 Gy) on the percentage of recapture by day of *C. pomonella* males in pheromone-baited (1 mg of codlemone) wing traps in July 2003. Approximately 3,260 males of each treatment were released per hectare on 10 July 2003 into four 1-ha plots. Trap density was five traps per hectare, which represented 20 traps total. Temperature line shows mean nightly temperature during the experiment. Means within each day denoted by asterisk are significantly different (PROC ANOVA; $P = 0.05$).

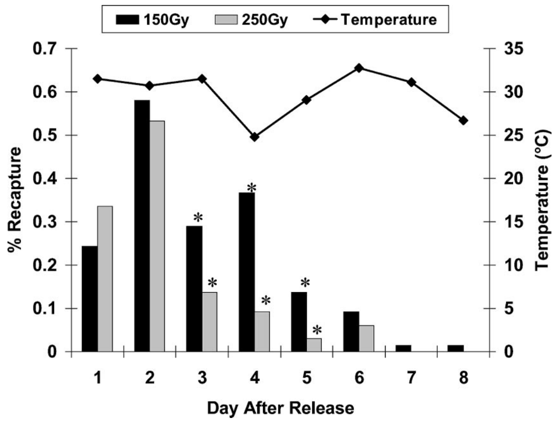

Fig. 6. Effect of dose of radiation (150 or 250 Gy) on the percentage of recapture by day of *C. pomonella* males in virgin female-baited wing traps in July 2003. Approximately 3,260 males of each treatment were released per hectare on 10 July 2003 into four 1-ha plots. Trap density was 16 traps per hectare, which represented 64 traps total. Temperature line shows mean nightly temperature during the experiment. Means within each day denoted by asterisk are significantly different (PROC ANOVA; $P = 0.05$).

were captured in four of the 8 d that data were collected. The difference was significant on day 2 ($F = 4.81$; df = 1, 180; $P < 0.0296$) (Fig. 5). In addition, the number of 150-Gy-treated males captured was higher than the number of 250-Gy-treated males in seven of 8 d that data were collected. The difference in capture was significant on day 3 ($F = 4.95$; df = 1, 180; $P < 0.0274$), day 4 ($F = 10.37$; df = 1, 180; $P < 0.0015$), and day 5 ($F = 5.14$; df = 1, 180; $P < 0.0246$) (Fig. 6). As stated above, the effect of dose of radiation on male recapture was slightly delayed with respect to the effect of rearing strategy (Figs. 5 and 6).

The individual and combined effects of rearing strategy (diapause or standard) and dose of radiation (150 or 250 Gy) on recapture of male codling moths in virgin female-baited traps and on the total number of males found in copula with females in mating tables in July 2003 are shown in Table 1. Both diapause rearing and lower dose of radiation increased male recapture by calling females in female-baited traps. When these effects are combined (Table 1), a radia-

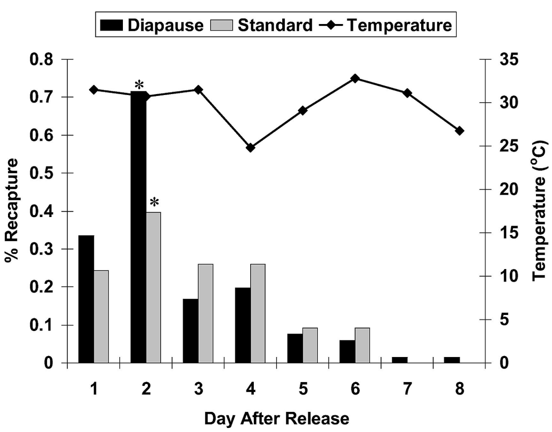

Fig. 5. Effect of mass-rearing strategy (diapause or standard) on the percentage of recapture by day of *C. pomonella* males in virgin female-baited wing traps in July 2003. Approximately 3,260 males of each treatment were released per hectare on 10 July 2003 into four 1-ha plots. Trap density was 16 traps per hectare, which represented 64 traps total. Temperature line shows mean nightly temperature during the experiment. Means within each day denoted by asterisk are significantly different (PROC ANOVA; $P = 0.05$).

Table 1. Individual and combined effects of mass-rearing strategy (diapause or standard) and dose of radiation (150 or 250 Gy) on percentage of recapture of *C. pomonella* males in virgin female-baited traps (VFBT) and on the number of males found in copula with females in mating tables (MT) in summer (July) 2003

Treatment	% recapture in VFBT[a]	No. matings in MT (n = 96)[b]
Individual effects		
Diapause rearing	1.570	
Standard rearing	1.356	
150 Gy	1.737	
250 Gy	1.189	
Combined effects		
Diapause 150 Gy	1.859	23
Diapause 250 Gy	1.280	24
Standard 150 Gy	1.616	31*
Standard 250 Gy	1.097	18*

Approximately 1,630 males of each treatments were released per hectare on 10 July 2003 into four 1-ha plots. Trap densities were as follows: for VFBT, 16 traps per hectare (64 traps) and for MT, 32 traps per hectare (64 traps) total.

[a] Statistical differences in percentage of recapture in the virgin female-baited traps are indicated in Figs. 5 and 6.

[b] Asterisk (*) denotes significant difference between means (Student's t-test, $P = 0.0406$).

tion dose-response in recapture is evident for male codling moths reared through both rearing strategies. The number of matings was not significantly different for diapause-reared males treated with 150 or 250 Gy. However, standard-reared males obtained a significantly (t = 2.982, df = 4, P = 0.0406) higher mean (±SD) number of mates per night when treated with 150 Gy (6.20 ± 1.92) than when treated with 250 Gy (3.60 ± 1.52).

A total of 96 males were collected in copula with females in mating tables during the five nights of this study. The majority of matings (59.4 and 34.4%) were observed when the mating tables were visited at 2200 and 2300 hours, respectively. No significant interaction was detected between the number of matings by each male type and the time of night when the mating occurred. An examination of the pattern of hourly recapture of male codling moths in mating tables and pheromone-baited and female-baited traps revealed no significant interactions between trap type and number of males captured each hour. Most of the males found in synthetic pheromone traps (37.8 and 25.2% of a total of 365 males) and all of the males found in virgin female-baited traps (77.8 and 22.8% of a total of 36 males) also were captured during 2200 and 2300 hours, respectively. This time corresponds with the time when female codling moths are most actively mating in the orchard.

Discussion

Trapping of *C. pomonella* has been used to augment control; assess moth density; examine phenology, dispersal, and behavior; and evaluate the success of various control strategies (Weissling and Knight 1994). Furthermore, many sterile insect release programs evaluate the field performance and competitiveness of colony insects by using release-recapture tests (Henneberry and Keaveny 1985, Lance et al. 1988). This study is the first to examine the combined effects of rearing strategy and dose of radiation on the field performance of mass-reared male *C. pomonella.* Our study was designed in a way that would allow us to measure various aspects of field competitiveness by recapturing males in traps with strong (synthetic) and weak (virgin female) sex pheromone signals and by capturing them in copula with females in mating tables. Because pheromone-baited traps constantly emit a synthetic sex pheromone signal, they have the potential to capture males well before and after those that are attracted by females in virgin-baited traps or in mating tables. As such, synthetic pheromone-baited traps can better measure differences among male treatments with respect to their readiness and ability to respond to sexual signals early in the evening and to remain active late into the night—an indication of their general quality. Also, compared with the traps baited with virgin females, these traps measure the ability of males to respond from greater distances because they are active for a longer period (continuous pheromone release) and the pheromone signal is (≈10 times) stronger. In comparison, virgin female-baited traps test the relative ability of males to respond to a weak pheromone source that may be emitted intermittently and only during a specific time of the day. Mating tables baited with clipped wing virgin females test the same competitive attributes of a male as are tested by virgin female-baited traps. However, mating tables are more selective because only the most competitive male, i.e., the one that reaches the female the quickest and interacts with her using the appropriate behaviors, will be able to successfully mate with the female. Virgin female-baited sticky traps, however, can (theoretically) capture all of the males that respond to the calling female.

Even though each of these field sampling methods are useful in measuring slightly different aspects of male performance and competitiveness, traps (especially pheromone-baited traps) more easily collect higher numbers of males and, therefore, may provide a better opportunity to detect differences among male treatments. Our results show that the quality of sterile released male codling moths is significantly improved both by rearing the insects through diapause and by treating them with a lower dose of radiation (150 Gy). The fact that significantly more diapaused codling moths were recaptured than moths reared under constant temperature was not altogether unexpected. Proverbs (1971) had previously reported that moths reared in the laboratory from egg to adult at a constant high temperature were less active than wild moths in the spring. Hutt (1979) reported that field competitiveness of laboratory-reared moths was improved when fluctuating temperatures were used. Mass rearing through diapause simply goes one step further in more closely approximating natural field conditions. As reported in previous studies (Bloem et al. 1998), the beneficial effects of diapause rearing were observed not only in the spring (May) when evening temperatures were low but also in July when evening temperatures remained high. The benefits of using the lowest possible dose of radiation to sterilize released moths are also well known (North and Holt 1968, Toba et al. 1972, Carpenter et al. 1997). For the codling moth, Bloem et al. (1999b, 2001) have previously reported improvements in trap recapture rates, mating competitiveness, and dispersal ability at lower doses of radiation.

Similar to the results reported in Bloem et al. (1998, 2001), we recaptured a higher percentage of released moths in pheromone-baited traps during the summer than we did in the spring, irrespective of insect treatment. Results in the summer showed a more "typical" pattern of recapture, i.e., codling moth males were captured in high numbers for the first 3–4 d. The decline in percent recapture from day 6–11 was most likely influenced by insect movement and mortality (Figs. 3 and 4). In contrast, percentage of recapture in the spring was attenuated on days 3–5 when mean nightly temperatures were below 17°C. However, codling moths remained in the orchard and again became active when nightly temperatures increased (days 6–10) (Figs. 1 and 2).

These positive effects on field performance were observed regardless of the field sampling method used (i.e., pheromone-baited traps, virgin female-baited traps, or mating tables baited with virgin females). We found significant interactions between larval rearing strategy and dose of radiation with respect to recapture day after release. Larval rearing strategy influenced male performance immediately after field release. However, the benefit of using a lower dose of radiation was not observed until 2–3 d after release. In general, the best-performing males were those that were mass reared through diapause and received a low dose of radiation (150 Gy). It is worth noting that the difference in male performance due to dose of radiation was greater when males were reared through standard rearing protocols, suggesting that rearing through diapause might attenuate some of the negative effects of higher doses of radiation (250 Gy). We are currently conducting complementary laboratory evaluations to examine whether this attenuation has a measurable physiological basis. The results presented here and in earlier studies (Bloem et al. 1998) continue to suggest that future areawide programs for codling moth should consider designing mass-rearing facilities where the colony is routinely reared through diapause. This study also contributes to the mounting body of evidence that indicates that lowering the dose of gamma radiation used to treat the laboratory populations has a significant positive effect on field performance and on the ultimate success of the areawide program.

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References Cited

Bloem, K. A., and S. Bloem. 2000. Sterile Insect Technique for codling moth eradication in British Columbia, Canada, pp. 207–214. *In* Ken-Hong Tan [ed.], Area-Wide Control of Fruit Flies and Other Insect Pests. Proceedings of the FAO/IAEA Symposium. Penang, Malaysia, 1998. Penerbit University Sains Malaysia, Penang, Malaysia.

Bloem, S., and J. E. Carpenter. 2001. Evaluation of population suppression by irradiated Lepidoptera and their progeny. Fla. Entomol. 84: 165–171.

Bloem, S., K. A. Bloem, and S. L. Fielding. 1997. Mass-rearing and storing codling moth larvae in diapause: a novel approach to increase production for sterile insect release. J. Entomol. Soc. Br. Columbia 94: 75–81.

Bloem, S., K. A. Bloem, and A. L. Knight. 1998. Assessing the quality of mass-reared codling moths (Lepidoptera: Tortricidae) by using field release-recapture tests. J. Econ. Entomol. 91: 1122–1130.

Bloem, S., K. A. Bloem, J. E. Carpenter, and C. O. Calkins. 1999a. Inherited sterility in codling moth (Lepidoptera: Tortricidae): effect of substerilizing doses of radiation on insect fecundity, fertility and control. Ann. Entomol. Soc. Am. 92: 1–8.

Bloem, S., K. A. Bloem, J. E. Carpenter, and C. O. Calkins. 1999b. Inherited sterility in codling moth (Lepidoptera: Tortricidae): effect of substerilizing doses of radiation on field competitiveness. Environ. Entomol. 28: 669–674.

Bloem, S., K. A. Bloem, and C. O. Calkins. 2000. Incorporation of diapause into codling moth mass-rearing: production advantages and insect quality issues, pp. 329–335. *In* Ken-Hong Tan [ed.], Areawide Control of Fruit Flies and Other Insect Pests. Proceedings of the FAO/IAEA Symposium. Penang, Malaysia, 1998. Penerbit Universiti Sains Malaysia, Penang, Malaysia.

Bloem, S., K. A. Bloem, J. E. Carpenter, and C. O. Calkins. 2001. Season-long releases of partially sterile males for control of codling moth, *Cydia pomonella* (Lepidoptera: Tortricidae), in Washington apples. Environ. Entomol. 30: 763–769.

Brinton, F. E., M. D. Proverbs, and B. E. Carty. 1969. Artificial diet for mass production of the codling moth, *Carpocapsa pomonella* (Lepidoptera: Olethreutidae). Can. Entomol. 101: 577–584.

Calkins, C. O., and T. R. Ashley. 1989. The impact of poor quality of mass-reared Mediterranean fruit flies on the sterile insect technique used for eradication. J. Appl. Entomol. 108: 401–408.

Carpenter, J. E., Hidryani, Novri Nelly, and B. G. Mullinix. 1997. Effect of substerilizing doses of radiation on sperm precedence in fall armyworm (Lepidoptera: Noctuidae). J. Econ. Entomol. 90: 444–448.

Dendy, C., M. G. Powell, and Associates Ltd. 2001 A Study of the Financial Sustainability of the Okanagan-Kootenay SIR Program for the Control of Codling Moth Post 2005. Report prepared for the Okanagan Valley Tree Fruit Authority and the Okanagan-Kootenay SIR Board, Part I: 17 pp. + appendices, Part II: 23 pp. + appendices.

Dyck, V. A., S. H. Graham, and K. A. Bloem. 1993. Implementation of the sterile insect release programme to eradicate the codling moth, *Cydia pomonella* (L.) (Lepidoptera: Olethreutidae), in British Columbia, Canada, pp. 285–297. *In* Proceedings of the FAO/IAEA Symposium, Vienna, 1992. International Atomic Energy Agency, Vienna, Austria.

Henneberry, T. J., and D. F. Keaveny. 1985. Suppression of pink bollworm by sterile moth releases. USDA–ARS. ARS-32.

Huettel, M. D. 1976. Monitoring the quality of laboratory reared insects: a biological and behavioral perspective. Environ. Entomol. 5: 807–814.

Hutt, R. B. 1979. Codling moth (*Laspeyresia pomonella*) (Lepidoptera: Olethreutidae): improving field performance of mass-reared males. Can. Entomol. 111: 661–664.

LaChance, L. E. 1985. Genetic methods for the control of lepidopteran species: status and potential. USDA–ARS. ARS-28.

Lance, D. R., T. M. Odell, V. C. Mastro, and C. P. Schwalbe. 1988. Temperature-mediated programming of activity rhythms in male gypsy moths (Lepidoptera: Lymantriidae): implications for the sterile male technique. Environ. Entomol. 17: 649–653.

North, D. T. 1975. Inherited sterility in Lepidoptera. Annu. Rev. Entomol. 20: 167–182.

North, D. T., and G. Holt. 1968. Inherited sterility on progeny of irradiated male cabbage loopers. J. Econ. Entomol. 61: 928–931.

Proverbs, M. D. 1971. Orchard assessment of radiation-sterilized moths for control of *Laspeyresia pomonella* (L.) in British Columbia, pp. 117–133. *In* Proceeding IAEA application of induced sterility for control of lepidopterous populations, Vienna, Austria. International Atomic Energy Agency, Vienna, Austria.

SAS Institute. 1989. SAS user's guide. SAS Institute, Cary, NC.

Toba, H. H., A. N. Kishaba, and D. T. North. 1972. Reduction of populations of caged cabbage loopers by release of irradiated males. J. Econ. Entomol. 65: 408–411.

Weissling, T. J., and A. L. Knight. 1994. Passive trap for monitoring codling moth (Lepidoptera: Tortricidae) flight activity. J. Econ. Entomol. 87: 103–107.

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